

DESCRIPTIONS OF A NEW SPECIES AND THREE INCOMPLETELY
KNOWN SPECIES OF WESTERN NEARCTIC *ISOPERLA*
(PLECOPTERA: PERLODIDAE)

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Abstract.—The male, female, nymph, and egg of *Isoperla miwok*, new species, are described from a Sierra Nevada intermittent stream, California. Distinguishing features include male aedeagal shape and spination, female subgenital plate shape, adult and nymphal pigment patterns, and microstructure of the collarless egg. This new species is placed in the *Isoperla sobria* (Hagen) complex. The male aedeagus, female, nymph, and egg of *Isoperla acula* Jewett are described, and this species is moved to the *Isoperla quinquepunctata* (Banks) complex. Males have a unique patch of sclerotized scales encircling the aedeagus near the apex. Other features include the triangular subgenital plate of the female, the pigment pattern of the nymph, and the collarless egg. *Isoperla acula* is closely related to *Isoperla mormona* Banks, but differs by inhabiting small intermittent streams. Nymphs of *Isoperla adunca* Jewett and *Isoperla bifurcata* Szczytko and Stewart are described, and both species are retained in the *Isoperla sordida* Banks complex. *Isoperla adunca* nymphs are unique among western Nearctic *Isoperla* species by lacking longitudinal abdominal stripes.

Key Words: Plecoptera, Perlodidae, *Isoperla*, new species, western Nearctic species complexes

Twenty-two species of *Isoperla* are currently known from the western Nearctic region (Stark et al. 1986), and relationships within this group have been elucidated in recent revisions by Szczytko and Stewart (1979, 1984). Using morphological characters of adults, nymphs, and eggs, they erected five species complexes for 20 *Isoperla* species, and two species remained unassigned. Placement of some species within these complexes was tentative because certain life stages were unknown. Presently, one male, one female, ten nymphs, and two eggs of the 22 *Isoperla* species are unknown or incompletely described. Szczytko and Stew-

art (1979) have stressed the desirability of completing these life stage descriptions for a better understanding of phylogenetic relationships in this group. Further descriptions of several *Isoperla* species endemic to California are especially needed because this region is important in the group's evolution, past dispersal, and zoogeography.

During a study of stoneflies in the central Sierra Nevada of California, we collected and associated many adults and nymphs of *Isoperla*. In the process, a new species was discovered, plus the undescribed life stages of three rarely collected species were collected, *Isoperla acula* Jewett (male aede-

gus, female adult, nymph, and egg), *Isoperla adunca* Jewett (nymph), and *Isoperla bifurcata* Szczytko and Stewart (nymph).

The objectives of this paper were to (1) describe all life stages of a new *Isoperla* species from California, (2) complete the descriptions of all life stages of *I. acula*, *I. adunca*, and *I. bifurcata*, and (3) relate these new data to the five *Isoperla* species complexes.

MATERIALS AND METHODS

This study was based on collections of *Isoperla* nymphs and adults from many habitats in the Cosumnes River basin (sea level to 2249 m elevation) on the western slope of the central Sierra Nevada, California. Positive nymph/adult associations of all four species were made by rearing mature nymphs to emergence in the field and/or laboratory using small growth containers. Cool water temperatures (4–12°C) were necessary to maintain *I. bifurcata* nymphs until they emerged, but the other three species collected from low elevation habitats emerged successfully at much warmer water temperatures (15–29°C). Teneral adults were held in the laboratory to obtain eggs.

Adult and nymphal drawings were made with a Wild M5-A stereo dissecting microscope and camera lucida. The microstructures of nymphal mouthparts, terga, and eggs were examined using compound and scanning electron microscopes (SEM). Eggs oviposited into holding containers or dissected from preserved gravid females were prepared for SEM study as described by Szczytko and Stewart (1979), and micrographs were made with an ISI Super III SEM. Male terminalia were treated for study according to the methods of Szczytko and Stewart (1979). Aedeagal armatures were examined from temporarily mounted sections in glycerol, and were studied with a Zeiss Standard RA, Routine and Research compound microscope. To facilitate study of the males, the aedeagus of living specimens was everted just prior to preservation.

Voucher specimens of all four *Isoperla* have been deposited in the National Museum of Natural History (USNM), Washington, D.C.; California Academy of Sciences (CAS), San Francisco, Calif.; and Brigham Young University, Provo, Utah. Additional specimens are in the collections of S. W. Szczytko and R. L. Bottorff.

RESULTS AND DISCUSSION

Isoperla miwok Bottorff and Szczytko, NEW SPECIES

Male.—Macropterous. Body length 8–10 mm; forewing length 7.5–9.5 mm, slightly exceeding abdomen. General body color light to medium brown. Dorsum of head creamy yellow, dark band connecting median and lateral ocelli; interocellar area light; light spot anterior to median ocellus; occiput light brown behind lateral ocelli, with reticulations (Fig. 1). Antennae brown, pedicel and scape margins dark. Pronotum with light median stripe, disks medium brown, rugosities dark, anterior and posterior margins dark, anterolateral corners light (Fig. 1). Meso-metanota with light median stripe or spot anteriorly. Wings light brown. Femora with light-dark distal bands. Abdominal terga with two mesal longitudinal rows of dots. Vesicle absent. Paraprocts pointed, deflected outward at tips, recurved over posterior margin of tenth tergum, slightly crenulated and bearing short setae (Figs. 2, 3). Aedeagus membranous with expanded balloon-like apical section bearing 2 small rounded lobes and a long, narrow, tail-like, anteromedian tube (difficult to see and evert in preserved specimens) covered with fine rounded spinulae (Fig. 4B) and a postero-median truncated lobe void of spinulae (Fig. 4); posteroapical patch of large, heavy, reddish brown spines (Fig. 4C); mesal area covered with stout, evenly spaced, proximally projecting, golden brown spinulae (Fig. 4A) and posterior band of large, heavy, proximally projecting, reddish brown spines which grade into smaller, lighter spines

proximally (Fig. 4D); proximal area with fine shallow scales bearing microtrichia and small fine spinulae (Fig. 4E). Cercal segments with a long posteroventral seta.

Female.—Macropterous. Body length 10–12 mm; forewing length 9–11 mm, slightly exceeding abdomen. Body color and external morphology similar to male. Subgenital plate truncate, wide at base, produced at least $\frac{1}{2}$ length over 9th sternum; posterior $\frac{1}{3}$ dark brown, posterior margin evenly rounded; scattered long fine hairs mesally (Fig. 5).

Nymph.—Body length of mature nymph 10–14 mm. General body color medium brown. Dorsum of head with a dark wide lateral band between ocelli and antennal bases, which extends anterolaterally and encloses a small light spot; interocellar area light; triangular light area anterior to median ocellus connecting to transverse light band across frontoclypeus, posterior corners of triangle extending as thin light lines to antennal bases; epicranial suture light; occiput bearing irregular row of short spinulae (Fig. 6). Lacinia triangular, bidentate; 1 axillary seta; 8–9 long marginal setae below subapical tooth (1 thin seta at tooth base, then 7–8 equally-spaced stout setae); 2 long stout submarginal setae below base of main tooth; sparse marginal and submarginal fine setae extending to lacinia base (Figs. 7, 8). Mandibles with 6 teeth, outer 3 teeth serrated; wide ventral patch of long setae extending between base of outer tooth and mandibular base, inner mandibular surface with row of long stout marginal setae (Figs. 9, 10); mandibles with brush of stout setae from base of inner teeth to marginal setal row (left mandible brush dense and medium length, right mandible brush sparse and short) (Figs. 11, 12). Antennae 80–100% of body length, 60–69 segments. Pronotal median stripe, lateral margins, and rugosities light; disks brown; margins fringed with short to long setae; angles rounded (Fig. 6). Legs with a dorsal fringe of long fine hairs; dark band distally on femora, proximally

on tibia. Abdominal terga with 3 longitudinal brown stripes, 1 mesal and 2 lateral; anterior and posterior margins dark; 8 longitudinal rows of dots, 2 mesal and 3 each laterally (Fig. 6). Cerci 70–80% of body length; 28–31 segments, each with posterior whorl of short setae, and one long dorsal and ventral seta; complete dorsal fringe of long hairs after 17th segment.

Egg.—Length 400–450 μm ; width 300–350 μm . General shape a prolate spheroid, cross section circular (Fig. 13). Color white. Collar and eclosion line absent (Fig. 13). Chorion covered with irregularly rounded to hexagonal follicle cell impressions (FCI's); FCI walls thick, raised; FCI floors flat with 3–5 medium-sized aeropyles (Fig. 14). Micropylar row subequatorial; orifices with small lips, positioned on FCI floors and walls, some associated with rosettes of 4–5 FCI's (Fig. 14).

Distribution.—This species is known only from the Sierra Nevada foothills, California.

Types.—Holotype male, allotype female, and three paratype nymphs collected from California, El Dorado Co., Indian Creek, 3.3 km NE of Michigan Bar bridge, 13-IV-1987, R. L. Bottorff, deposited in the National Museum of Natural History, Washington, D.C. Paratypes (R. L. Bottorff, collector).—California: Amador Co.: Little Indian Creek, 3 km W of Plymouth, 1 female 18-IV-1986, 1 female 9-V-1986. El Dorado Co.: Indian Creek, 3.3 km NE of Michigan Bar bridge, 97 nymphs 25-III-1987, 21 males, 4 females, 79 nymphs, 6 males & 1 female lab-reared 8-IV-1987, 2 males, 3 females lab-reared 9-IV-1987, 2 males, 4 females lab-reared 11-IV-1987, 17 males, 8 females, 49 nymphs 13-IV-1987, 2 males, 4 females lab-reared 20-IV-1987, 1 male, 2 females lab-reared 23-IV-1987, 1 nymph 10-III-1988; unnamed creek tributary to N bank of Cosumnes River, 2.9 km upstream of Michigan Bar bridge, 4 males, 5 females, 2 nymphs 9-IV-1986, 1 female lab-reared, 1 nymph 10-IV-1986, 2 males

lab-reared 11-IV-1986, 2 females lab-reared 15-IV-1986; unnamed creek tributary to N bank of N Cosumnes River, 6 km N Nashville, 1 exuvium 1-V-1987, Sacramento Co.: Burgoyne Creek, 1.3 km NE of Michigan Bar bridge, 1 male, 1 female 9-IV-1986, 1 female lab-reared 10-IV-1986, 1 female lab-reared 22-IV-1986, 1 nymph 25-III-1987; Cosumnes River at Michigan Bar, 1 nymph 27-I-1982, 2 nymphs 5-III-1982, 1 nymph 23-IV-1982, 1 male 22-III-1984, 1 male 14-IV-1984, 1 female 22-IV-1984, 1 male, 1 female 11-IV-1986, 1 male 18-IV-1986, 1 male, 1 female 29-IV-1986, 1 male lab-reared 31-III-1986, 1 male lab-reared 5-IV-1986, 1 male & 1 female lab-reared, 1 nymph 11-IV-1986; Cosumnes River at Sloughhouse, 1 nymph 5-III-1982; unnamed creek tributary to S bank of Cosumnes River, 0.3 km upstream of Michigan Bar bridge, 2 males 29-III-1986, 1 male lab-reared, 1 nymph 30-III-1986, 1 female lab-reared 31-III-1986, 1 nymph 25-III-1987. Paratypes are in the collections of the California Academy of Sciences, Brigham Young University, S. W. Szczytko and R. L. Bortorff.

Etymology.—This species is named in honor of the Miwok tribe of California Indians, whose tribal area includes the type locality.

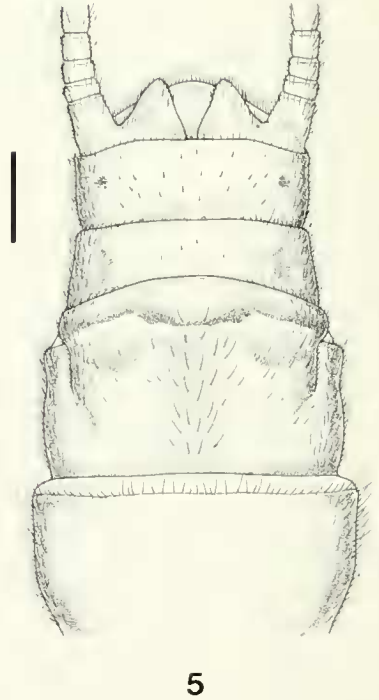
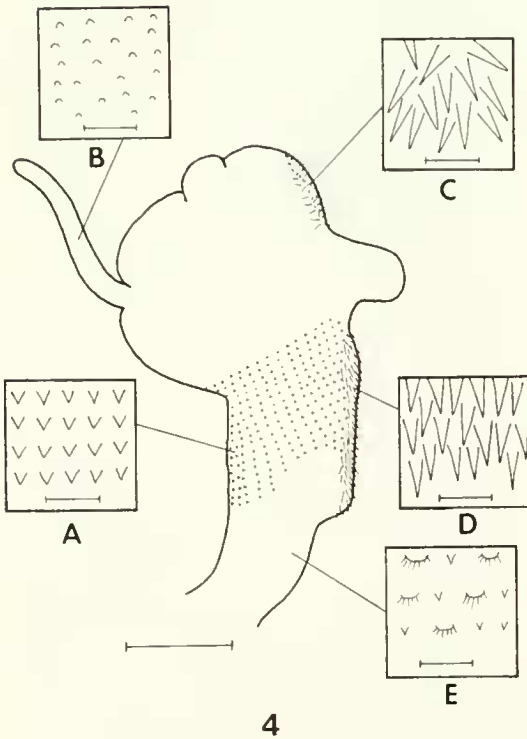
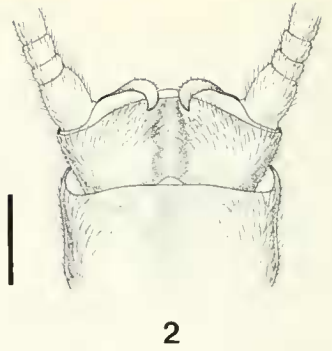
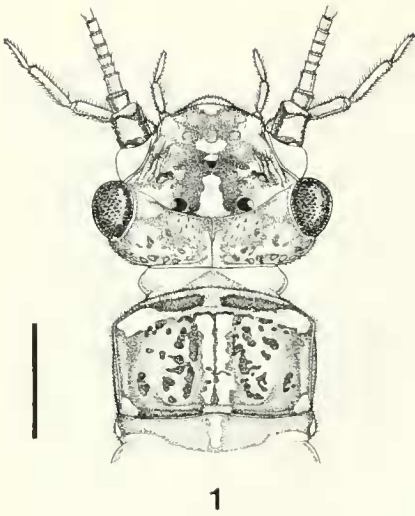
Biological notes.—*Isoperla miwok* primarily occurred in small intermittent streams at lower elevations (20–350 m) of the Sierra Nevada foothills, California. Only a few nymphs were found in nearby larger perennial streams despite extensive searching in these habitats. When this species emerged in March and April, the intermittent streams had low flow and warm water (23–29°C), causing nymphs to exhibit a “push-up” behavior to aid oxygen uptake. Although microhabitats of coarse substrate and fast current were present, mature nymphs usually were collected from pools which had aquatic macrophytes and a silty substrate. Nymphs held in the laboratory several days or weeks at room temperatures (20–25°C) and without water current nor-

mally emerged successfully. Emergence started in late March, reached a peak in mid April, and finished by early May, soon after which the stream habitat completely dried. Other Plecoptera found in these intermittent streams included, *Isoperla acula*, *I. adunca*, *Oemopteryx vanduzeei* (Claassen), *Suwallia* (new species), *Sweltsa californica* (Jewett), and more rarely, *Cosumnoperla hypocrena* Szczytko and Bortorff. *Isoperla miwok* emerged several weeks before *I. acula* and *I. adunca*.

Diagnosis.—*Isoperla miwok* is placed in the *Isoperla sobria* (Hagen) complex, which has three other western Nearctic species (Szczytko and Stewart 1979): *I. gravitans* (Needham and Claassen), *I. sobria*, and *I. tilasqua* Szczytko and Stewart. It shares the following characteristics with these species: (1) a large body size, (2) male aedeagus membranous, tubular, and bearing patches of small stout spinulae and longer hair-like spinulae, (3) male vesicle reduced or absent, (4) female subgenital plate truncate or broadly rounded, wide at base, and (5) egg chorion with evenly spaced aeropyles. The male aedeagus of *I. miwok* is most similar to *I. tilasqua* because both have a long apical tube(s). However, *I. miwok* can be separated from all members of this species complex by the pigment patterns of adults and nymphs, the shape and spinule pattern of the male aedeagus, the single long tube on the aedeagus, the shape and pigment of the female subgenital plate, and the collarless egg.

The egg of *I. miwok* is most similar to *I. acula* because both lack a collar and have raised FCI walls, but can be distinguished by its larger overall size, fewer aeropyles in the FCI floors, micropyles with small lips, and some micropyles positioned in FCI floors.

Within this species complex, only *I. miwok* and *I. sobria* occur in California. Both species were found in the same major drainage basin, but were separated by stream type and elevation. *Isoperla miwok* occurred in



Figs. 1–5. *Isoperla miwok* adults. 1. Head and pronotum. 2. Male terminalia, dorsal. 3. Male paraproct, lateral. 4. Aedeagus, lateral; A, mesal band of short, stout golden brown spinulae; B, fine rounded spinulae on anteromedian tail-like tube; C, posteroapical patch of large, heavy reddish brown spines; D, posteromesal patch of large, heavy, proximally projecting reddish brown spines; E, proximal patch of fine, shallow scales with microtrichia and fine spinulae. 5. Female subgenital plate, ventral. Scale lines: 1 = 1 mm; 2, 4, and 5 = 0.5 mm; 3 = 0.2 mm; 4A, B, C, D, and E = 25 μ m.

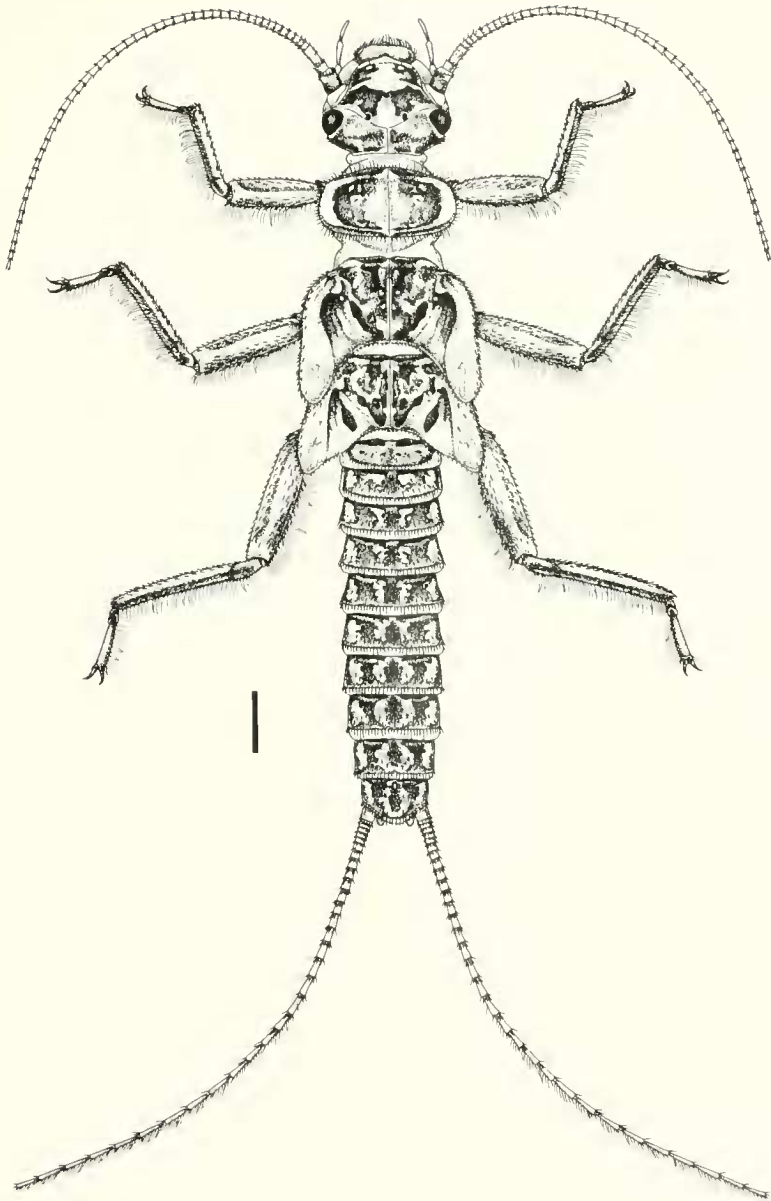


Fig. 6. *Isoperla miwok*, mature nymph, habitus; scale line = 1 mm.

low elevation, intermittent, small streams, while *I. sobria* occurred in medium or high elevation, perennial, small streams. *Isoperla miwok* coexisted with *I. acula* and *I. adunca*, which are in different species complexes, emerged later, and have different drumming calls (Bottorff et al. in press).

Isoperla acula Jewett

Isoperla acula Jewett 1962: 18. Holotype male; Fresno Co., California (CAS).
Isoperla acula Illies 1966: 393.
Isoperla acula Szczytko and Stewart 1979: 77.

Male.—Jewett (1962) and Szczytko and Stewart (1979) have described the male external morphology of *I. acula*. Aedeagus with narrow apical tubular section with sclerotized patch of flat scales which are finely divided anteriorly (Fig. 15B), apex with a small nipple, spinulae absent (Fig. 15); large anteromedian lobe with narrow anterior band of small, fine spinulae (Fig. 15A); mesal section void of spinulae; area below mesal section covered with stout, evenly spaced, proximally projecting, golden brown spinulae (Fig. 15C); proximal area with fine, shallow scales bearing microtrichia (Fig. 15D).

Female.—Macropterous. Body length 10–13 mm; forewing length 11–12.5 mm. Body color and external morphology similar to male. Subgenital plate triangular, produced posteriorly $\frac{1}{2}$ length over 9th sternum; apex variable (normally narrowly rounded, but some broadly rounded, pointed, or rarely notched); mesal patch of long fine setae (Fig. 16).

Nymph.—Body length of mature nymph 10–14 mm. General body color medium brown, covered with dark clothing hairs. Dorsum of head with strongly contrasting pigment pattern (Fig. 17); dark lateral bands extend from ocelli to antennal bases, then anterolaterally; triangular light spot anterior to median ocellus connecting to thin transverse light band across frontoclypeus; interocellar area light; posterior margin of head dark brown, with dark curved bands extending anteriorly to lateral ocelli; stem of epicranial suture light; large irregular light area between each compound eye and lateral ocellus; occiput bearing sinuous row of short spinulae (Fig. 17). Lacinia triangular, bidentate; 1 axillary seta; 20–25 marginal setae below subapical tooth (1 thin seta at tooth base, then 6–8 long equally-spaced stout setae, then 12–16 smaller setae); 3 long stout submarginal setae below base of main tooth, then a narrow continuous band of fine submarginal setae to lacinia base (Figs. 18, 19). Mandibles with 6 teeth, most ser-

rated; wide ventral patch of long setae extending between base of outer tooth and mandibular base, inner mandibular surface with row of long stout marginal setae (Figs. 20, 21); mandibles with brush of stout setae from base of inner teeth to marginal setal row (left mandible brush dense and medium length, right mandible brush sparse and short) (Figs. 22, 23). Pronotum with median stripe, disk stripes, and lateral margins light; anterior and posterior margins dark; margins fringed with short and occasional long setae; angles rounded (Fig. 17). Meso-metanota each with 4 dark pointed bars extending posteriorly from anterior margin toward 2 isolated dark bars (Fig. 17). Thoracic sternum with numerous chloride cells (Fig. 26). Legs with a dorsal fringe of long fine hairs; tibia with proximal dark spot. Abdominal terga with 3 longitudinal dark brown bands, median band narrow, lateral bands wide and flared anteriorly and posteriorly (Fig. 17); anterior margin dark; posterior fringe of medium-long setae and scattered intercalary spinulae (Figs. 17, 27, 28). Cercal segments with posterior whorl of short setae; complete dorsal fringe of long hairs after 17th segment.

Egg.—Length 350–370 μ m; width 230–260 μ m. General shape a prolate spheroid, cross section circular (Fig. 24). Color cream. Collar and eclosion line absent (Fig. 24). Chorion covered with irregularly rounded to pear-shaped FCI's; FCI walls thick, raised; FCI floors flat and finely punctate with 18–28 small aeropyles (Fig. 25). Micropyles subequatorial, associated with rosettes of 4–5 FCI's (Fig. 25).

Distribution.—This species is known only from the Sierra Nevada foothills, California.

Material examined.—California (R. L. Bottorff, collector, except where noted): Amador Co.: Big Indian Creek, 6 km N of Plymouth, 1 male 13-VI to 9-VIII-1982, R. Fouch, 7 nymphs 11-IV-1986, 1 female lab-reared 22-IV-1986, 1 female lab-reared 24-IV-1986, 2 females, 2 nymphs 25-IV-1986,

2 males, 2 females lab-reared 28-IV-1986, 1 male, 3 females 9-V-1986, 1 male lab-reared 12-V-1986, 2 males lab-reared 14-V-1986, 3 females lab-reared 16-V-1986, 1 female lab-reared 17-V-1986, 1 female lab-reared 26-V-1986, 1 female 30-V-1986, 3 nymphs 25-III-1987, 1 female lab-reared, 7 nymphs 1-V-1987; Little Indian Creek, 3 km W of Plymouth, 3 nymphs 18-IV-1986, 11 nymphs 25-IV-1986, 1 male, 2 females 29-IV-1986, 1 female 9-V-1986, 2 males, 1 female 30-V-1986, 24 nymphs 25-III-1987, 18 nymphs 1-V-1987, 6 males, 12 females lab-reared 4-V-1987, 8 males, 9 females, 1 nymph 12-V-1987. Butte Co.: 9 mi. N Oroville, 1 male, 5 nymphs 24-IV-1955, S. W. Hitchcock (USNM). El Dorado Co.: Acorn Creek, 6 km S Pilot Hill, 8 nymphs 3-IV-1988; Cooper Canyon, 3 km W Pilot Hill, 26 nymphs 2-IV-1988; Deadman Creek, 3.8 km SE of El Dorado, 6 nymphs 1-V-1987; Knickerbocker Creek, 5 km NW Pilot Hill, 35 nymphs 6-II-1988; Skunk Canyon, 6 km S Pilot Hill, 1 nymph 3-IV-1988; Sweetwater Creek, 10 km S Pilot Hill, 20 nymphs 3-IV-1988; unnamed creek tributary to N bank of N Cosumnes River, 6 km N Nashville, 5 nymphs 1-V-1987, 90 nymphs 12-V-1987; unnamed creek tributary to Folsom Lake at Rattlesnake Bar, 6 km SW Pilot Hill, 2 nymphs 2-IV-1988. Fresno Co.: Dry Creek, 7 mi. NE of Academy, 1 male (Holotype, CAS) 19-IV-1955, D. L. Abell. Sacramento Co.: Cosumnes River at Michigan Bar, 1 nymph 5-III-1982, 1 nymph 23-IV-1982, 1 male 31-V-1982.

Biological notes.—*Isoperla acula* primarily occurred in small intermittent streams at lower elevations of the Sierra Nevada foothills, California (see Biological Notes for *I. miwok*). Only a few nymphs were found in nearby larger perennial streams. It co-existed with *I. adunca* and *I. miwok*, both members of other *Isoperla* species complexes. Emergence started in mid April, reached a peak in early May, and finished by late May.

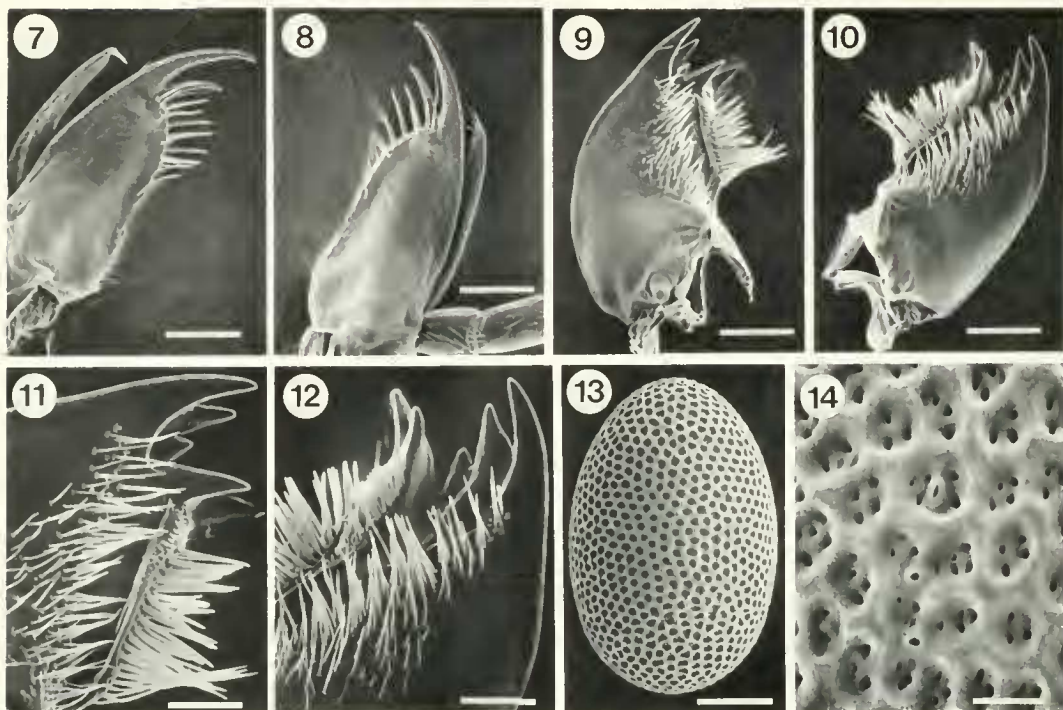
Diagnosis.—The phylogenetic relation-

ships of *I. acula* have remained unclear since the original description of the male because of the incomplete aedeagal description, the scarcity of specimens, and the undescribed female, nymph, and egg. Szczytko and Stewart (1979) tentatively placed *I. acula* in the *I. sordida* complex based on the male pigment pattern and Jewett's (1962) partial description of an aedeagal sclerotized structure. It is now clear that *I. acula* males have a band of sclerotized scales which encircle the aedeagus apex, but lack the distinctive sclerotized process which projects from the membranous aedeagus of all species in the *I. sordida* complex.

Isoperla acula should be included in the *I. quinquepunctata* (Banks) complex, which includes four other western Nearctic species: *I. jewetti* Szczytko and Stewart, *I. longiseta* Banks, *I. mormona* Banks, and *I. quinquepunctata* (Szczytko and Stewart 1979). It shares the following characteristics with these species: (1) 9th and/or 10th male abdominal terga with patches of stout hairs or spinulae, (2) a row of occipital spinulae on nymphal head, (3) a dorsal fringe of long hairs on nymphal legs, and (4) three longitudinal stripes on abdominal terga of nymphs.

Isoperla acula is closely related to *I. mormona* based on similarities in the shape and spination of the male aedeagus, in the bipartite patch of spinulae on the male 9th tergum, and in the pigment patterns of the adult and nymphal head-pronotum. Nymphs will key to *I. mormona* in Szczytko and Stewart (1979). However, *I. acula* can be distinguished from this species by (1) a band of sclerotized scales on the aedeagus, (2) a male vesicle wider than long, (3) male paraprocts long and thin, (4) a triangular female subgenital plate which is produced over sternum 9, (5) larger sized nymphs and adults, and (6) eggs lacking a collar, but with distinct FCI walls.

Isoperla mormona occurs throughout the western Nearctic region, while *I. acula* is restricted to California (Szczytko and Stewart 1979).



Figs. 7-14. *Isoperla miwok* nymph and egg. 7, Right maxilla, ventral. 8, Left maxilla, ventral. 9, Right mandible, ventral. 10, Left mandible, ventral. 11, Detail of right mandible, ventral. 12, Detail of left mandible, ventral. 13, Egg. 14, Detail of egg chorion and micropyles. Scale lines: 7, 8, 9, and 10 = 0.2 mm; 11, 12, and 13 = 0.1 mm; 14 = 20 μ m.

art 1979). Both species occur at low elevations in the Sierra Nevada, but emerge at different times and inhabit distinctly different stream types. *Isoperla acula* inhabited small intermittent streams, while *I. mormona* inhabited large perennial rivers. The morphological similarity of the two species suggests a recent divergence, possibly associated with the drier climates and increasingly intermittent flow conditions in small streams of the Sierra Nevada foothills following the Pleistocene epoch. Most stoneflies in this region emerge prior to the summer warming of streams; however, *I. mormona* is one of the last to emerge, often when water temperatures exceed 20°C in June-July. The ability of *I. mormona* nymphs to cope with warm water temperatures in perennial streams may have pre-adapted variants for life in nearby inter-

mittent streams and led to the recent evolution of *I. acula*. The male drumming calls of these two morphologically-similar species are distinctly different in beat number and interval, suggesting that drumming behavior has diverged faster than morphological traits and has been an important isolating factor (Bottorff et al. in press).

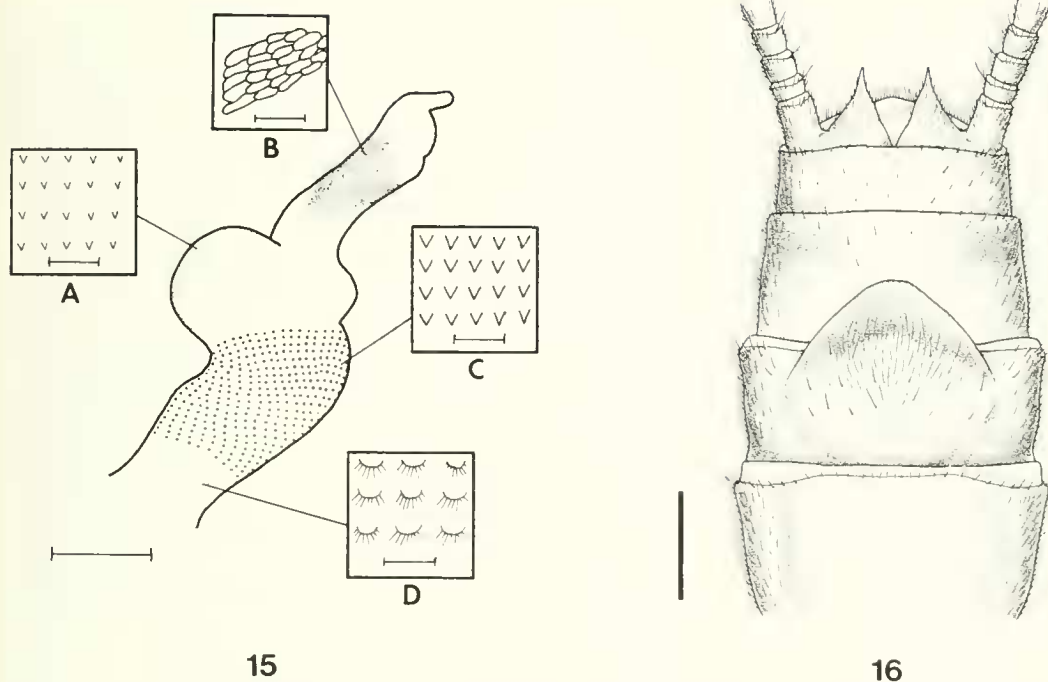
Isoperla adunca Jewett

Isoperla adunca Jewett 1962: 19. Holotype male, allotype female; Santa Clara Co., California (CAS).

Isoperla adunca Illies 1966: 393.

Isoperla adunca Szczytko and Stewart 1979: 80.

Nymph.—Body length of mature nymph 9–12 mm. General body color uniform medium brown. Dorsum of head with a square



Figs. 15–16. *Isoperla acula* adults. 15, Aedeagus, lateral; A, anteromedian band of small fine spinulae; B, sclerotized patch of flat scales; C, patch of stout, evenly spaced, proximally projecting golden brown spinulae; D, proximal patch of fine, shallow scales with microtrichia. 16, Female subgenital plate, ventral. Scale lines: 15 and 16 = 0.5 mm; 15A, B, C, and D = 25 μ m.

light spot anterior to median ocellus, spot margined laterally by medium brown anteriorly-pointed lobes; light lines extend between lobes and antennal bases; small light spot anterior to lateral ocelli; frontoclypeus with a light transverse band; center of interocellar area light; occiput with reticulations and an irregular row of short spinulae which is interrupted medially (Fig. 29). Lacinia quadrate, bidentate, small gap between bases of main and subapical teeth; 1 axillary seta; definite marginal shelf below subapical tooth with 10–12 stout setae (6–7 long, 4–5 shorter); 8–9 long stout submarginal setae below main tooth, first 3 in gap; scattered marginal and submarginal fine setae extending to lacinia base (Figs. 30, 31). Mandibles with 6 teeth, most serrated; narrow ventral row of long setae extending between base of outer tooth and mandibular

base, inner mandibular surface with row of long stout marginal setae (Figs. 32, 33); mandibles with brush of stout setae from base of inner teeth to marginal setal row (left mandible brush dense and medium length, right mandible brush sparse and short) (Figs. 34, 35). Antennae light; margin of scape dark. Pronotum uniform brown, lateral margins light; rugosities darker than disks; margins fringed with short and occasional long setae; angles rounded (Fig. 29). Mesometanota brown, with a few light reticulations. Thoracic sterna with mesal sclera lacking dense hairs; membranes with chloride cells (Fig. 37). Legs with a dorsal fringe of long fine hairs. Abdominal terga uniform brown, becoming lighter near pleura, each segment with scattered intercalary spinulae and a posterior fringe of medium length setae (Fig. 36). Cercal segments with a pos-

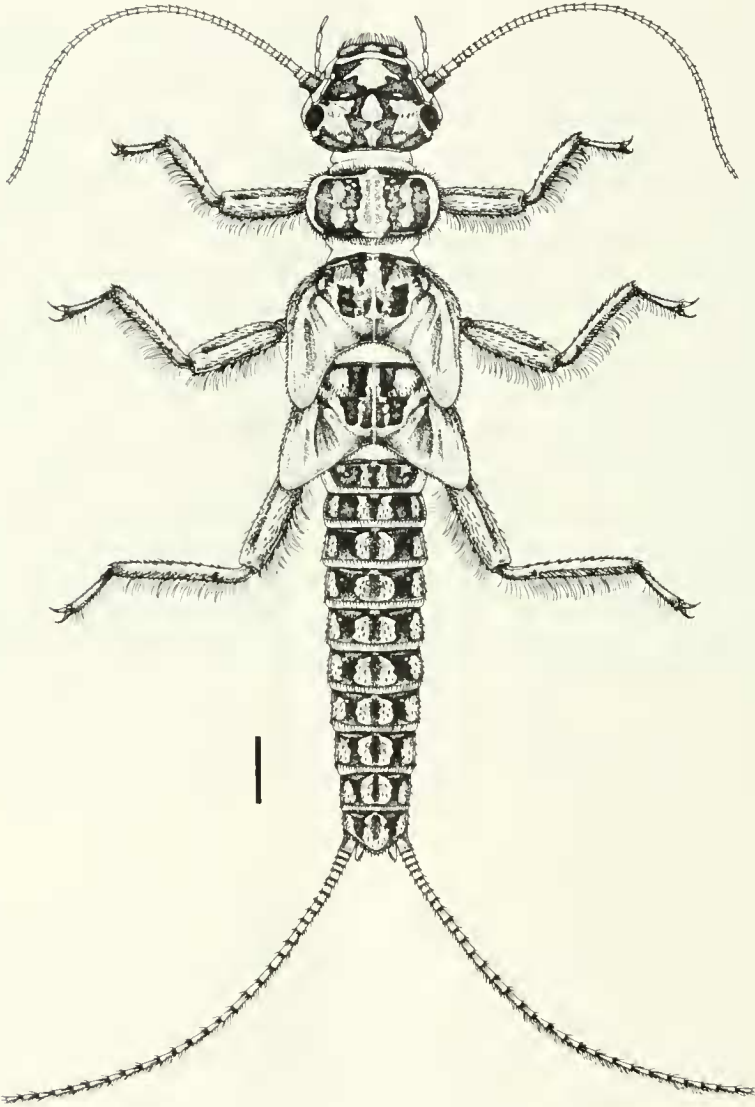


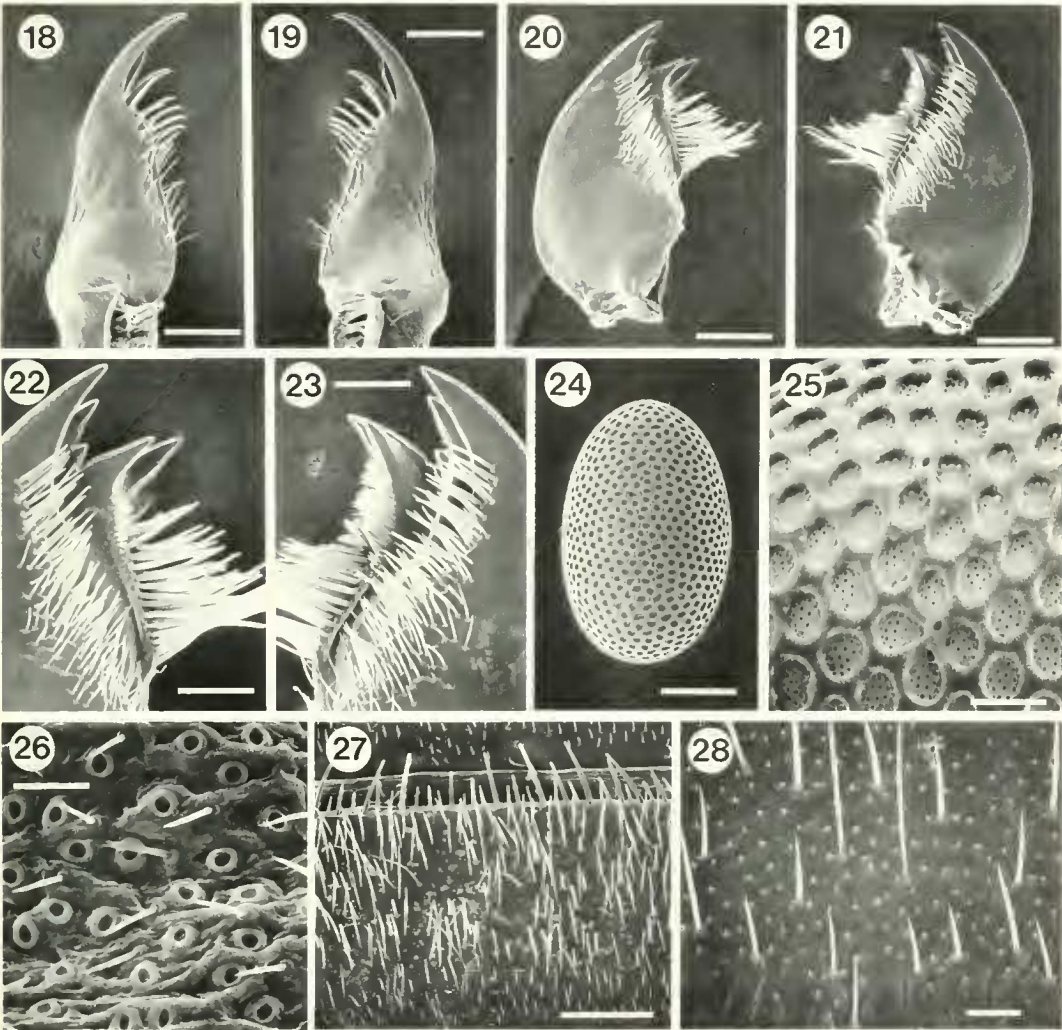
Fig. 17. *Isoperla acula*, mature nymph, habitus; scale line = 1 mm.

terior whorl of short setae and 1 long dorsal and ventral seta; sparse intrasegmental setae, continuous dorsal fringe absent.

Distribution.—This species is known only from the Sierra Nevada foothills and the Coast Range, California.

Material examined.—California (R. L. Bottorff, collector): Amador Co.: Big Indian Creek, 6 km N of Plymouth, 3 nymphs 25-IV-1986, 1 female, 3 nymphs 9-V-1986, 1

female lab-raised 10-V-1986, 1 male, 1 female lab-raised 12-V-1986, 1 female lab-raised 13-V-1986, 4 males, 6 females, 1 nymph 30-V-1986, 2 nymphs 1-V-1987; Little Indian Creek, 3 km W of Plymouth, 10 nymphs 18-IV-1986, 1 male, 5 nymphs 25-IV-1986, 1 male lab-reared, 2 nymphs 27-IV-1986, 1 male, 2 females 9-V-1986, 2 males, 6 females, 5 nymphs 30-V-1986, 2 males, 1 female lab-reared 31-V-1986, 5



Figs. 18–28. *Isoperla acula* nymph and egg. 18, Right lacinia, ventral. 19, Left lacinia, ventral. 20, Right mandible, ventral. 21, Left mandible, ventral. 22, Detail of right mandible, ventral. 23, Detail of left mandible, ventral. 24, Egg. 25, Detail of egg chorion and micropyles. 26, Chloride cells on thoracic sternum. 27, Abdominal terga. 28, Detail of abdominal tergum. Scale lines: 18, 19, 20, 21, and 27 = 0.2 mm; 22, 23, and 24 = 0.1 mm; 25, 26, and 28 = 20 μ m.

nymphs 25-III-1987, 3 males, 4 females 1-V-1987, 13 males, 8 females, 62 nymphs 12-V-1987. El Dorado Co.: Acorn Creek, 6 km S Pilot Hill, 1 nymph 3-IV-1988; Cooper Canyon, 3 km W Pilot Hill, 7 nymphs 2-IV-1988; Indian Creek, 3.3 km NE of Michigan Bar bridge, 34 nymphs 25-III-1987, 50 nymphs 8-IV-1987, 1 male, 48 nymphs 13-IV-1987, 1 male, 4 nymphs 21-

IV-1987, 6 nymphs 10-III-1988; unnamed N. bank tributary to Cosumnes River, 2.9 km upstream of Michigan Bar bridge, 16 nymphs 9-IV-1986; unnamed creek tributary to N bank of N Cosumnes River, 6 km N Nashville, 6 nymphs 1-V-1987, 53 nymphs 12-V-1987; unnamed creek tributary to Folsom Lake at Rattlesnake Bar, 6 km SW Pilot Hill, 13 nymphs 2-IV-1988.

Sacramento Co.: Burgoyne Creek, N bank tributary to Cosumnes River, 1.3 km upstream of Michigan Bar bridge, 25 males, 25 females, 27 nymphs 9-IV-1986, 1 male, 1 female lab-raised 10-IV-1986, 1 female 1-V-1986, 6 nymphs 25-III-1987; Cosumnes River at Michigan Bar, 7 nymphs 5-III-1982, 30 nymphs 23-IV-1982, 3 nymphs 21-VI-1982; Cosumnes River at Sloughhouse, 1 nymph 24-IV-1982; unnamed S bank tributary to Cosumnes River 0.3 km upstream of the Michigan Bar bridge, 13 nymphs 21-III-1986, 18 nymphs 29-III-1986, 1 female lab-reared 2-IV-1986, 4 males, 4 females, 10 nymphs, 1 male lab-reared 11-IV-1986, 17 males, 13 females 29-IV-1986, 15 nymphs 25-III-1987; unnamed S bank tributary Cosumnes River 0.7 km downstream of the Michigan Bar bridge, 2 nymphs 14-III-1986, 1 female lab-reared 26-III-1986, 1 male lab-reared 28-III-1986.

Biological notes.—*Isoperla adunca* primarily occurred in small intermittent streams at lower elevations of the Sierra Nevada foothills, California (see Biological Notes for *I. miwok*). Only a few nymphs were found in nearby larger perennial streams. Emergence usually started in late March and extended through April–May, but varied somewhat in different intermittent streams and years as influenced by water temperature and flow duration.

Diagnosis.—Based on the nymphal morphology described in this study, *I. adunca* is retained in the *I. sordida* complex. All nymphs in this group have a pronotal fringe of short stout hairs and occasional longer hairs (Szczytko and Stewart 1979). Additionally, most nymphs in this complex lack a continuous dorsal fringe of long cercal hairs. Based on adult characters, Szczytko and Stewart (1979) found *I. adunca* most closely related to *I. denningi* Jewett; however, the nymph of *I. denningi* is unknown.

Szczytko and Stewart (1979) stated that most Isoperlinae nymphs can be separated from the Perlodinae by the presence of

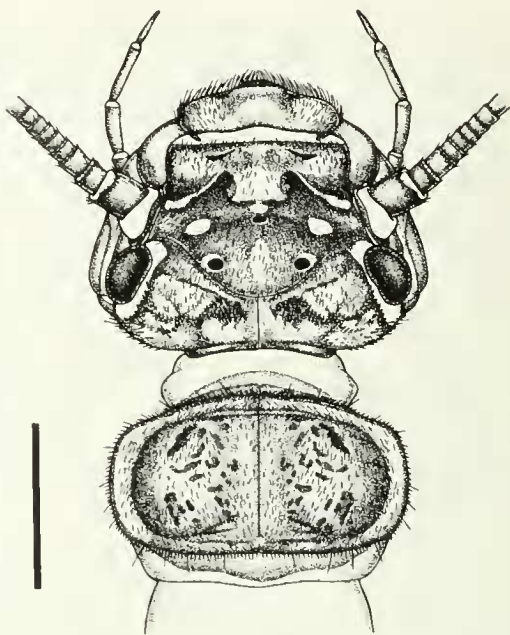
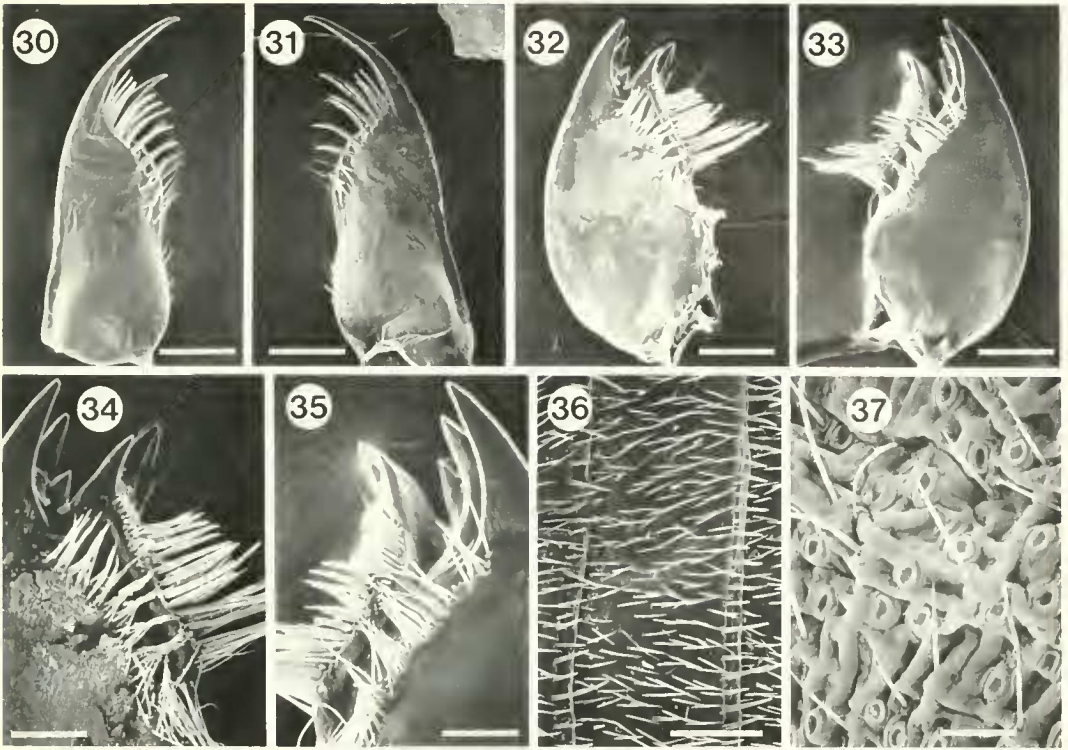


Fig. 29. *Isoperla adunca*, mature nymph, head and pronotum; scale line = 1 mm.

nymphal abdominal stripes. In contrast to all other western Nearctic *Isoperla*, *I. adunca* nymphs are unique in lacking longitudinal abdominal stripes (some eastern Nearctic species also lack abdominal stripes, including *I. burksi* Frison, *I. marlynia* (Needham and Claassen), and *I. signata* (Banks)). *Isoperla adunca* nymphs also differed from the other *Isoperla* in this study in their mouthpart setation and shape. The lacinia of *I. adunca* has a broad marginal shelf and numerous stout submarginal setae, while their mandibles have a narrow row of ventral setae. These differences were unexpected because Szczytko and Stewart (1979) reported little interspecific variation in the nymphal mouthparts of western Nearctic *Isoperla*.

In the central Sierra Nevada of California, *I. adunca* and *I. bifurcata*, members of the same species complex, occurred in the same major drainage basin, but they emerged at different times and inhabited different stream types. *Isoperla adunca* occurred in



Figs. 30–37. *Isoperla adunca* nymph. 30, Right lacinia, ventral. 31, Left lacinia, ventral. 32, Right mandible, ventral. 33, Left mandible, ventral. 34, Detail of right mandible, ventral. 35, Detail of left mandible, ventral. 36, Abdominal terga. 37, Chloride cells on thoracic sterna. Scale lines: 30, 31, 32, 33, and 36 = 0.2 mm; 34 and 35 = 0.1 mm; 37 = 20 μ m.

low elevation, intermittent, small streams, while *I. bifurcata* occurred in medium or high elevation, perennial, headwater springs. *Isoperla adunca* coexisted with *I. acula* and *I. miwok*, which are in different species complexes and have different drumming calls (Bottorff et al. in press).

Isoperla bifurcata Szczytko and Stewart

Isoperla sordida Gaufin et al. 1966: 71.

Isoperla sordida Gaufin et al. 1972: 119.

Isoperla sordida Baumann et al. 1977: 152.

Isoperla bifurcata Szczytko and Stewart 1979: 80. Holotype male, allotype female; Union Co., Oregon (USNM).

Nymph.—Body length of mature nymph 10–13 mm. General body color medium

brown, with a median light stripe extending longitudinally along entire dorsum, membranes of fresh specimens reddish and densely covered with chloride cells. Dorsum of head with a dark brown square-shaped band connecting ocelli, dark triangular patches extend posteriorly over occiput; center of interocellar area light; frontoclypeus with a light transverse band; light M-shaped line anterior to median ocellus; large oval light spot posterior to and small light spot anterior to lateral ocelli; occiput with an irregular row of short spinulae (Fig. 38). Lacinia triangular, bidentate; 1 axillary seta; 12–16 marginal setae below subapical tooth (1 fine seta at subapical tooth base, then 5–6 long equally-spaced stout setae, then 6–9 smaller setae); 3 long stout submarginal se-

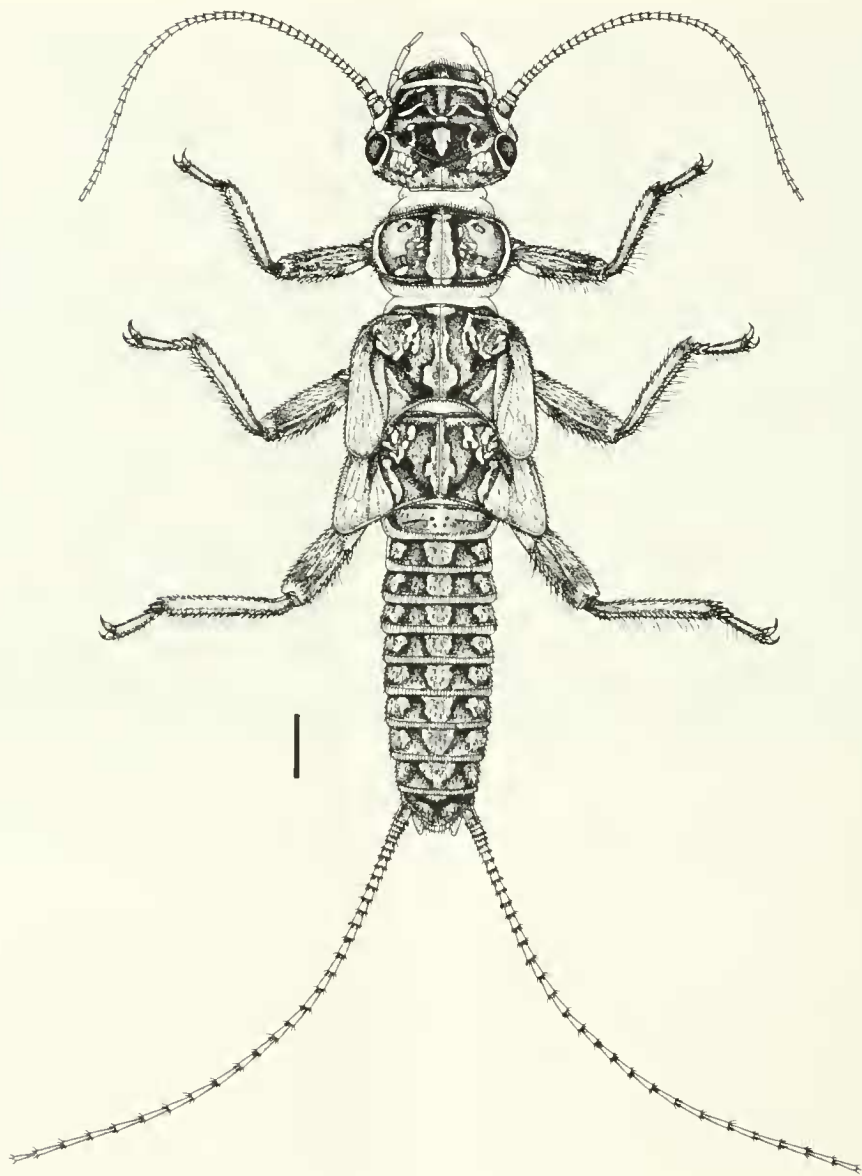


Fig. 38. *Isoperla bifurcata*, mature nymph, habitus; scale line = 1 mm.

tae below base of apical tooth; sparse row of fine marginal and submarginal setae extending to lacinia base (Figs. 40, 41). Mandibles with 6 teeth, most serrated; wide ventral patch of long setae extending between base of outer tooth and mandibular base, inner mandibular surface with row of long stout marginal setae (Figs. 42, 43); mandi-

bles with brush of stout setae from base of inner teeth to marginal setal row (left mandible brush dense and medium length, right mandible brush sparse and short) (Figs. 44, 45). Pronotum with light median stripe bordered by dark brown stripes, lateral margins and rugosities light, disks light brown, anterior and posterior margins dark; margins

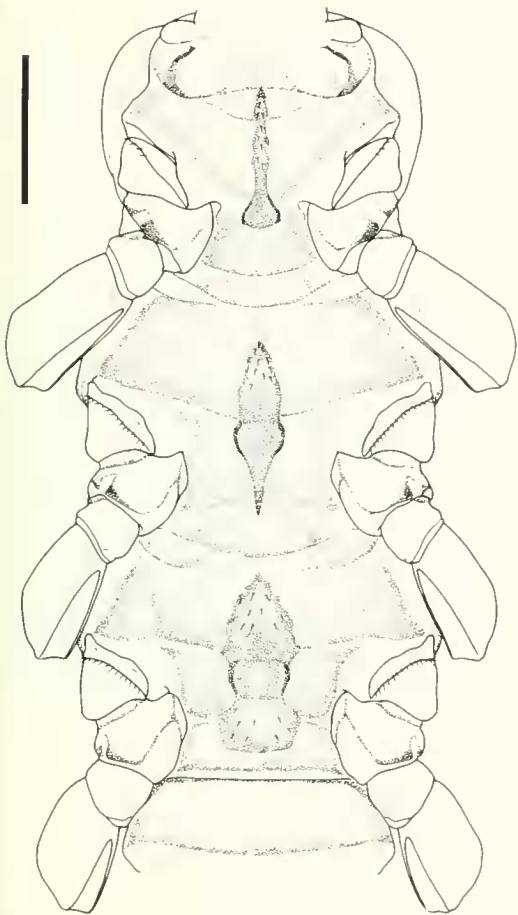


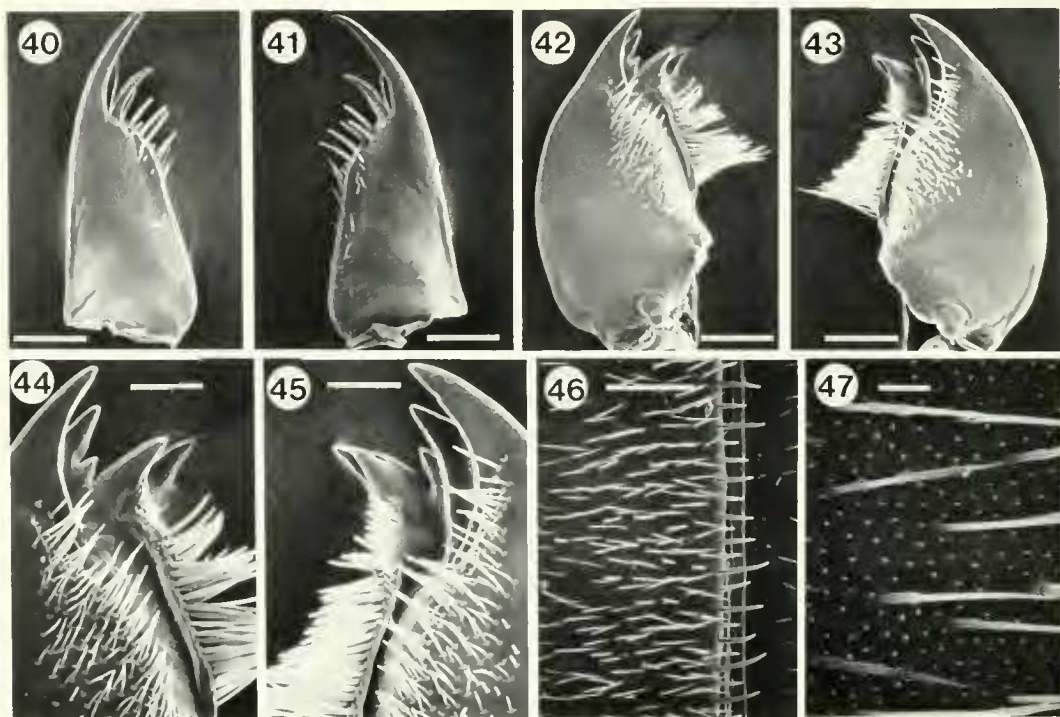
Fig. 39. *Isoperla bifurcata* nymph, thoracic sternite; scale line = 1 mm.

fringed with short stout setae and occasional long setae; angles rounded (Fig. 38). Meso-metanota with light median stripe and reticulations. Meso-metasterna with distinct mesal sclera with dark clothing hairs and patches of stout spinulae (Fig. 39). Legs with sparse dorsal fringe of fine hairs. Abdominal terga with longitudinal median light band and two lateral dark brown bands (Fig. 38); numerous long and short intercalary spinulae (Figs. 46, 47); posterior fringe of medium length setae. Cercal segments with a posterior whorl of short setae and longer ventral seta; sparse intrasegmental setae, continuous dorsal fringe absent.

Distribution.—This species is known from California, Idaho, Oregon, and Washington.

Material examined.—California (R. L. Bottorff, collector): El Dorado Co.: Singleton Springs at headwaters of N Cosumnes River, 25 km E of Grizzly Flat, 3 nymphs 6-VIII-1980, 2 nymphs 15-II-1981, 5 nymphs 27-III-1981, 21 nymphs 24-IV-1981, 10 nymphs 31-V-1981, 25 nymphs 2-X-1981, 15 nymphs 9-III-1982, 37 nymphs 20-IV-1982, 18 nymphs 17-V-1982, 15 nymphs 2-VII-1982; N Cosumnes River, 30–100 m downstream of Singleton Springs, 39 nymphs 6-VIII-1980, 1 female, 15 nymphs 5-IX-1980, 18 nymphs 24-IX-1980, 25 nymphs 31-X-1980, 5 nymphs 26-XII-1980, 6 nymphs 15-II-1981, 20 nymphs 27-III-1981, 6 nymphs 24-IV-1981, 1 nymph 31-V-1981, 109 nymphs 10-VII-1981, 1 male, 1 female, 7 nymphs 16-VIII-1981, 1 female in trap 16-VIII to 2-IX-1981, 74 nymphs 2-X-1981, 9 nymphs 15-XII-1981, 40 nymphs 16-I-1982, 42 nymphs 9-III-1982, 66 nymphs 20-IV-1982, 33 nymphs 17-V-1982, 1 male, 1 female, 59 nymphs 2-VII-1982, 5 males, 4 females 7-VII-1982, 1 male, 3 females 16-VII-1982, 1 male, 1 female 2-VIII-1982, 27 nymphs 10-VIII-1982, 1 female 23-VIII-1982, 12 nymphs 22-VI-1987, 1 male field-reared 9–16-VII-1987, 1 male, 2 females field-reared 16–26-VII-1987, 2 females field-reared 26-VII to 8-VIII-1987; unnamed spring stream tributary to N bank of N Cosumnes River, 2.4 km upstream of Meiss Ranch and 18 km E of Grizzly Flat, 5 nymphs 19-VI-1986, 9 nymphs 30-VI-1986, 15 nymphs 8-VI-1987, 1 male field-reared 8–22-VI-1987, 2 males, 2 females field-reared 22-VI to 9-VII-1987; unnamed N bank tributary to N Cosumnes River, 2.3 km upstream of Meiss Ranch and 18 km E of Grizzly Flat, 1 nymph 14-VI-1986, 1 nymph 18-VI-1986.

Biological notes.—*Isoperla bifurcata* occurred in small spring-fed streams (order 1–2) at medium or high elevations (>1500 m) in the Sierra Nevada, California, and nor-



Figs. 40–47. *Isoperla bifurcata* nymph. 40, Right lacinia, ventral. 41, Left lacinia, ventral. 42, Right mandible, ventral. 43, Left mandible, ventral. 44, Detail of right mandible, ventral. 45, Detail of left mandible, ventral. 46, Abdominal terga. 47, Detail of abdominal tergum. Scale lines: 40, 41, 42, 43, and 46 = 0.2 mm; 44 and 45 = 0.1 mm; 47 = 20 μ m.

mally did not coexist with other *Isoperla* species. Emergence started in mid June, reached a peak in July, and continued into August. A few adults were collected in early September, primarily ovipositing females. Other common stoneflies in these habitats included *Soyedina nevadensis* (Claassen) and *Sweltsa borealis* (Banks).

Diagnosis.—Based on the nymphal morphology described in this study, *I. bifurcata* is retained in the *I. sordida* complex because all members have similar pronotal and cercal setation. Szczytko and Stewart (1979) found a close relationship between adults of *I. bifurcata* and *I. fusca* Needham and Claassen. The nymphs of these two species share a similar pattern of longitudinal abdominal stripes and a reduced or absent dorsal fringe of leg hairs. *Isoperla bifurcata*

nymphs can be distinguished from all other members in this species complex by their pigment pattern, reduced dorsal fringe of leg hairs, and sclerotized thoracic sterna.

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